

Food Web Structure and the Evolution of Ecological Communities

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Abstract

Simulations of the coevolution of many interacting species are performed using the Webworld model. The model has a realistic set of predator-prey equations that describe the population dynamics of the species for any structure of the food web. The equations account for competition between species for the same resources, and for the diet choice of predators between alternative prey according to an evolutionarily stable strategy. The set of species present undergoes long-term evolution due to speciation and extinction events. We summarize results obtained on the macro-evolutionary dynamics of speciations and extinctions, and on the statistical properties of the food webs that are generated by the model. Simulations begin from small numbers of species and build up to larger webs with relatively constant species number on average. The rate of origination and extinction of species are relatively high, but remain roughly balanced throughout the simulations. When a ‘parent’ species undergoes speciation, the ‘child’ species usually adds to the same trophic level as the parent. The chance of the child species surviving is significantly higher if the parent is on the second or third trophic level than if it is on the first level, most likely due to a wider choice of possible prey for species on higher levels. Addition of a new species sometimes causes extinction of existing species. The parent species has a high probability of extinction because it has strong competition with the new species. Non-parental competitors of the new species also have a significantly higher extinction probability than average, as do prey of the new species. Predators of the new species are less likely than average to become extinct.

1 Introduction

In this article we discuss the Webworld model which, by describing the interaction of species over a wide range of timescales, allows us to start from

a very few species and evolve food webs which represent the predator-prey relationships amongst a large community of diverse species. A typical food web generated by the model is shown in Figure 1.

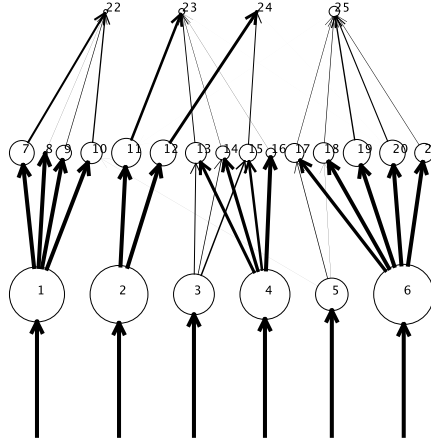


Figure 1: *Typical food web produced by the model*

The web shown in the figure is typical in the sense that the webs which are evolved by Webworld resemble real food webs by having very few predator-prey links between species on the same level, and also very few cycles; most of the links, and certainly the major ones, start on one level and end on a higher one. A more quantitative comparison between the model and ecological data confirms this broad similarity.

Webworld was designed as a model of an evolving community of many interacting species. It is intended to address questions of interest on both ecological and evolutionary timescales. Models of population dynamics accounting for predator-prey interactions between species work on the ecological scale. These date back to Lotka and Volterra and form a familiar part of the theoretical biology literature (Pielou, 1977; Roughgarden, 1979). Many studies have considered the dynamical behaviour and type of attractors that arise with systems of coupled equations representing a few (usually two or three) species (Emlen, 1984; Hallam, 1986; Hastings & Powell, 1991; McCann & Yodzis, 1994; Post *et al.* 2000). Some studies have addressed the problem of stability of these dynamical equations when many interacting species are present (May, 1974; Svirzhev & Logofet, 1983; Logofet, 1993; Hofbauer &

Sigmund, 1998). When one considers many species, the structure of the food web that connects them becomes relevant. Which species prey on which other species? Which species compete with one another for the same resources? Recent studies of general food web structures including these features have been carried out by Bastolla *et al.* (2000) and Lässig *et al.* (2001).

There is also a body of literature in theoretical biology that considers the statistical properties of food webs (Pimm, 1982), both as observed in the field (e.g. Hall & Raffaelli, 1991; Goldwasser & Roughgarden, 1993; Martinez & Lawton, 1995) and as predicted by various types of random graph models (Cohen, 1990; Cohen *et al.* 1990). These studies consider how many trophic levels there are in food webs, how the species are distributed between the levels, and how many predators and prey are possessed by each species in the web. Patterns such as these are static rather than dynamic, but it is clear that the arrangement of the links in the food web will influence the population dynamics, and that the community structure we observe has been created by the dynamics of the system, rather than being simply thrown together. We therefore require theoretical models that can address both static and dynamic questions.

In addition to the relatively rapid ecological dynamics, it is important to consider long-term evolutionary dynamics. Speciation will create new species and extinction will remove some of the old ones. When a new species arises, this will have knock-on effects on other species in the community through predation and competition interactions. There is the potential for indirect effects to influence many other species. There are now a large number of evolutionary models, mostly in the physics literature, that investigate the dynamics of extinction events and the possibility of large scale avalanches of extinctions. Mass extinctions are an important feature observed in the fossil record. Biologists have tended to ask what causes these events — climate changes, meteorite strikes etc. An idea stemming from the theory of self-organized criticality is that the dynamics of the system itself may be inherently unstable and subject to large scale avalanches of extinctions (Bak & Sneppen, 1993; Solé *et al.* 1997). Theoretical models of macro-evolution and extinction have been reviewed recently by Drossel (2001). It is not surprising that changes in the non-living environment of an ecosystem can sometimes have catastrophic effects on the living species. The key question here is what would the macro-evolutionary dynamics be like in the absence of external changes. Does evolution lead to communities of stable interacting species that cannot be replaced by new ones? Does it create a continual

turn-over of new species replacing old ones (a Red Queen scenario), or does it create critical food web structures prone to large scale fluctuations?

Webworld has been designed to fill a gap between the different types of models described above. Neither the models of food web structure or those of population dynamics consider evolution, whilst the macro-evolutionary models contain very little biological detail and often ignore population dynamics. The model we have arrived at involves lengthy computer simulations and is more complex than many of the other models referred to above. Whilst we recognize that simplicity is a virtue, we also feel that the level of detail included here has the payoff of allowing us to address a very wide range of biological questions. We also would like to resist the tendency to assume that effects observed in very simple models will always prove to be ‘universal’. We will argue that it is important to have qualitatively correct population dynamics, and point out cases where omitting seemingly unimportant effects, leads to significant changes in the biological conclusions.

The Webworld model has already been described in detail in Drossel *et al.* (2001) and Caldarelli *et al.* (1998), therefore we only describe it briefly in the following section. This paper will try to summarize some of the effects observed in simulations with Webworld in our previous papers, and will then focus on the question of what happens when a new species is added to a food web. Diagrams will be shown of a few representative cases, and new statistical results will be given describing the response of the web to a single speciation event.

2 Population Dynamics

Each species in the model is represented by a set of L features or phenotypic characters chosen from a set of K possible features. Typically $L = 10$ and $K = 500$ in the model, which means that the number of possible species is extremely large and evolution never runs out of scope for innovation. Each species has a “score” against any other species that is calculated as a function of the set of features possessed by each of the species. The score S_{ij} is positive if species i is adapted to prey on species j , and is zero if not. These scores are used as the numerical coefficients in the population dynamics equations discussed below.

Let the rate at which one individual of species i consumes individuals of species j be denoted by $g_{ij}(t)$. This is usually called the ‘functional response’,

and it depends in general on the population sizes. We suppose that the population size N_i of each species satisfies an equation of the form:

$$\frac{dN_i(t)}{dt} = -N_i(t) + \lambda \sum_j N_i g_{ij}(t) - \sum_j N_j g_{ji}(t). \quad (1)$$

The first term on the right represents a constant rate of death of individuals in absence of interaction with other species. The final term is the sum of the rates of predation on species i by all other species, and the middle term is the rate of increase of species i due to predation on other species. Where there is no predator-prey relationship between the species the corresponding rate g_{ij} is zero. The factor λ is less than 1, and is known as the ecological efficiency. It represents the fraction of the resources of the prey that are converted into resources of the predator at each stage of the food chain. Throughout this paper, we have taken $\lambda = 0.1$, a value accepted by many ecologists (Pimm, 1982).

The external environment is treated as an additional ‘species 0’. For primary producers, the middle term includes a non-zero rate g_{i0} of feeding on the external resources. External resources (e.g. sunlight) enter the ecosystem at a constant rate R . In the equations this is implemented by defining $N_0 = R/\lambda$, and keeping N_0 fixed. We have deliberately chosen the form of Eq. (1) to be the same for all species. We do not want to define different equations for primary producers, herbivores, and carnivores etc, because species can change their position in the ecosystem as it evolves, and most species are both predators and prey.

The most straightforward form for the functional response would be to have g_{ij} proportional to the prey population size N_j , as is the case in the Lotka-Volterra equations (Pielou, 1977; Roughgarden, 1979). A variety of other forms have been proposed that account for the fact that when prey are scarce or when many predators choose the same prey, competition between predators reduces the amount of prey available to each predator, whilst when prey are abundant, the consumption rate per predator must saturate rather than continue to increase indefinitely with the prey population size (Holling, 1959; Beddington, 1975; Huisman & De Boer, 1997). The form of the functional response used in the recent versions of Webworld is

$$g_{ij}(t) = \frac{S_{ij} f_{ij}(t) N_j(t)}{b N_j(t) + \sum_k \alpha_{ki} S_{kj} f_{kj}(t) N_k(t)}. \quad (2)$$

This is based on the ratio-dependent functional responses used by Arditi & Ginsburg (1989) and Arditi & Michalski (1995). We have described in detail in Drossel *et al.* (2001) how we generalized these studies to give equation (2). In the denominator, the sum runs over all the species that are predators of species j . The factor α_{ki} determines the strength of competition between species for the same resources. This depends on the degree of similarity between the species:

$$\alpha_{ij} = c + (1 - c)q_{ij}, \quad (3)$$

where c is a constant such that $0 \leq c < 1$, and where q_{ij} is the ‘overlap’, or fraction of features of species i that are also possessed by species j . This means that competition is strongest between similar species (or members of the same species), and is weaker for different species because they can use the resources in slightly different ways.

The factor f_{ij} is the fraction of its effort (or available searching time) that species i puts into preying on species j . These efforts must satisfy $\sum_j f_{ij} = 1$. We suppose that the efforts of any species i are chosen so that the gain per unit effort g_{ij}/f_{ij} is equal for all prey j . If this were not true, the predator could increase its energy intake by putting more effort into a prey with higher gain per unit effort. This choice of efforts leads to the condition

$$f_{ij}(t) = \frac{g_{ij}(t)}{\sum_k g_{ik}(t)}. \quad (4)$$

We showed (Drossel *et al.* 2001) that this choice is an evolutionarily stable strategy (ESS) (Parker & Maynard Smith, 1990; Reeve & Dugatkin, 1998). If the population has efforts chosen in this way, there is no other strategy with a different choice of efforts that can invade the population. Predator diet choice is often discussed using optimal foraging theory (Stephens and Krebs, 1986). The basic idea is that each predator maximises its individual rate of resource input. In our model, the success of the predators’ strategies is a function of predator population size and the strategies of the other predators. The ESS solution is not equivalent to maximizing the resource input for a single predator. In most other models of optimal foraging, there is no competition between predators, hence there is no distinction between the ESS and the strategy with maximal resource input rate.

There are only four principal parameters that determine the behaviour of the model: R , the rate of input of external resources; λ , the ecological efficiency; b , which controls the saturation level of the functional response;

and c , which controls the competition strength. All other quantities are generated automatically in the simulation. For example, the scores S_{ij} and the values α_{ij} are determined by the features of the species. The efforts are also determined at each time point in the dynamics by ensuring that they remain at their ESS value (see Drossel *et al.* 2001 for more details).

3 Evolutionary Dynamics

For any set of species in the web the population dynamics can be described using the above equations. Evolution in Webworld occurs by speciation events. An existing species is chosen at random to undergo speciation, and a new species is created that differs by one randomly chosen feature from the parent species. The population dynamics is then followed with the additional species until a new stable state is reached. Species whose population falls below a threshold of 1.0 are considered extinct and removed from the web. In this way, new species gradually replace older ones, and the number of species present rises and falls.

It is worth stressing that the features should not be thought of as having any genetic basis — they are purely phenotypic characteristics — nor should the random replacement of randomly chosen features be thought of as genetic mutations. We do not attempt to model the extremely complex process of speciation. Instead, we imagine observing the variation of the species in the system on such a coarse time scale that the process of speciation appears to be stochastic. This is the process that we are modelling when we randomly change features. Of course, there are several variants of the scheme which we have adopted which it could be argued might have done just as well. For instance, the parent could be chosen according to criteria dependent on population size or trophic level, and not purely at random, and the child might not always have just one modified feature. We hope in the future to check that changes such as these do not alter the general predictions of the model.

Results in this paper are obtained from 80 different runs of Webworld using the same set of parameters ($\lambda = 0.1$, $c = 0.5$, $b = 0.005$, and $R = 1.0 \times 10^5$). Each run lasted for 100000 speciation events. The mean number of species in these 80 runs is shown as a function of time in Figure 2. This shows a fairly rapid increase initially, followed by stabilization to a fairly constant state where speciations are balanced by extinctions. Our previous paper

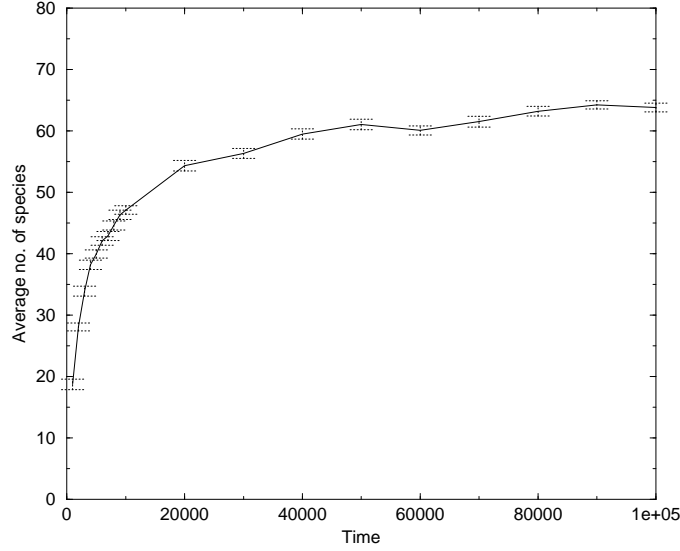


Figure 2: Mean number of species vs. time

(Drossel *et al.* 2001) shows the variation in the number of species in several individual runs. There is considerable fluctuation in each individual run, even at the later times when the average number is relatively constant. This shows that there is a continual turnover of species. There is considerable fluctuation between different runs with the same parameters due to the random choice of the feature that is changed at each speciation event.

Figures 3-6 show some examples of particular food webs generated by these simulations. In order to indicate population sizes, circles are shown with radius proportional to the log of the population size. Typical population sizes decrease by an order of magnitude on each successive trophic level. The arrows represent the flow of resources from prey to predator. The thickness of the arrow represents the amount of effort the predator puts into each prey. Many of the second and third level species split their effort between more than one prey. The level assigned to each species is determined by the shortest path to the external resources. For example, species 20 in Figure 3 is on level 2 because it feeds on species 6, which feeds on external resources. There are also longer pathways from species 20, via species 23 and 24. We use the shortest path to define the level because this can always be calculated unambiguously (even in the presence of cycles) and because longer pathways

provide relatively little resources. One observation from these webs is that the majority of interactions are simply between a prey species on one level and a predator on the level above (an ‘upward’ arrow in the diagrams). More complex situations, such as ‘downward’ or ‘horizontal’ arrows occur rarely.

In Figure 4, species 1-25 were in a state with stable populations. Species 1 has just undergone speciation to create the new species 26, which is also a level 1 species, like its parent. Figure 4 shows the situation after the population sizes have reached a new equilibrium. No extinction events have occurred. The population of species 26 has risen to be comparable to that of species 1. There is increased competition on level 1, hence some of the level 1 species populations have decreased (e.g. species 5). In Figure 3, species 1 had four predators feeding almost exclusively on it. When species 26 rises to a large population size, it pays these predators to put some of their effort into the new prey. This can be seen in Figure 4, where species 8 and 9 have switched predominantly to feeding on species 26, whilst species 7 has species 26 as a minor food source.

Another example is shown in Figures 5 and 6. Here we begin with the same 25 initial species, and species 26 arises on level 2, as a result of speciation of species 11. This new species causes the extinction of its parent species, 11, and three other species, 4, 16 and 24. The species that go extinct are all shaded in Figure 5. Figure 6 shows the situation after the new stable state is reached. This example shows that extinctions can occur on all levels, and that the nature of the interaction between the new species and the species that become extinct is not always straightforward. This point is pursued in the following section.

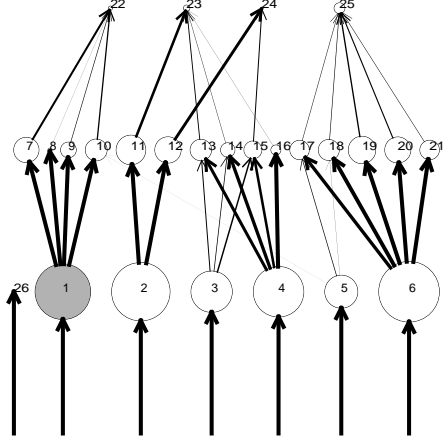


Figure 3: *Stable addition event: iteration 0*

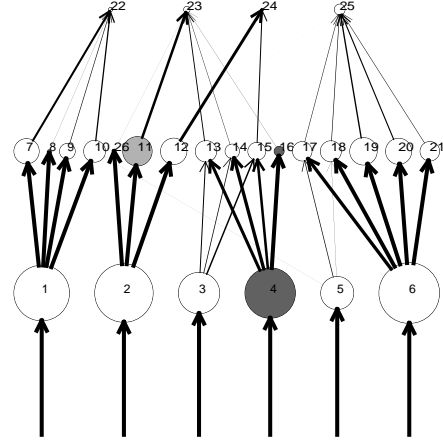


Figure 5: *Deletion event: iteration 0*

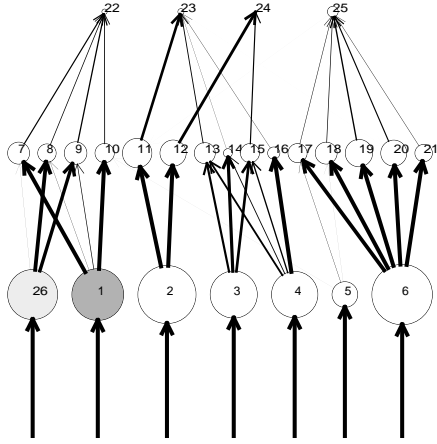


Figure 4: *Stable addition event: equilibrium*

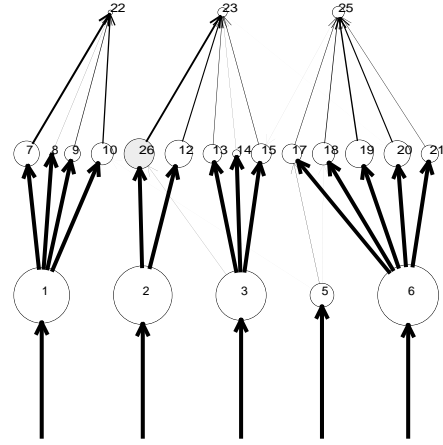


Figure 6: *Deletion event: equilibrium*

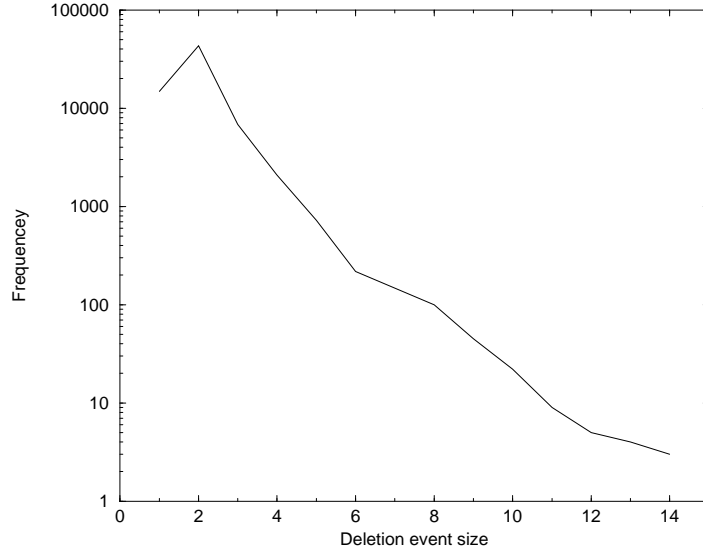


Figure 7: Deletion event size distribution

We referred to the continual turnover of species that occurs with this model. The main reason for this is that coevolutionary effects act both upwards and downwards in the web. New species on level one, for example, can out-compete older level 1 species, leading to their extinction, and possibly to the extinction of any level two species that fed on the old species (an upwards effect). However, a new level 2 species could arise that is a better adapted predator that causes its level 1 prey to go extinct (a downward effect). The way these effects operate depends on the form of the population dynamics equations. In our original paper (Caldarelli *et al.* 1998) we used a much simpler form of the population dynamics in which downward effects did not occur. We observed that the rate of turnover of species became slower and slower, and that the chance of a newly added species surviving decreased to virtually nil. Without downward effects, level one species can arise that are increasingly better adapted to the external environment, and it becomes increasingly more difficult to improve on them. With coevolutionary effects in both directions, species that are successful at one time do not remain successful for ever.

The sensitivity that we observed of the evolutionary dynamics to the short time scale population dynamics makes us somewhat sceptical of the results of

some of the simpler macro-evolutionary models in which there is essentially no population dynamics included at all. One question that has frequently been studied is the distribution of sizes of extinction events. Figure 7 shows the distribution of the number of species going extinct in each speciation event, given that at least one existing species goes extinct. The parameters are as for the runs in Figure 8. The majority of events are small, although the largest events (up to 14 species) represent a considerable fraction of the total number of species (average of 59 species per web). If we wished to look for evidence of critical phenomena it would be natural to ask how the size of the largest extinction events depends on the size of the web. However, in our model, the web size is not an independent parameter. We can increase the number of species by increasing the external resources, R , or decreasing the competition strength, c (see examples in Drossel *et al.* 2001). Computer time increases rapidly with the number of species, however, and it would be impractical to consider webs that were an order of magnitude larger than the present ones.

4 Food Web Properties and Co-evolution

For the same 80 runs discussed above, details of the web were stored at intervals of 10000 speciation events from time 10000 to 100000, thus giving 800 largely independent webs which we investigated in detail. Table 1 shows average properties of these webs. In this analysis a link was defined as being present if the effort of the predator against the prey was greater than 1%. Since the efforts are proportional to the consumption rates (because of the ESS criterion), this means that a link is counted if greater than 1% of the resources consumed by the predator come from the prey. This is slightly different to the definition used in our previous papers, which required g_{ij} to be greater than 1.0 for a link to be counted. The figures in Table 1 can be compared with those in Drossel *et al.* (2001), which use a range of different parameters, and those in Caldarelli *et al.* (1998), which were generated using a simpler form for the population dynamics equations.

In all the webs contributing to Table 1, the maximum trophic level present is either 3 or 4, with a mean of 3.85. The average level of all species is 2.31. The distribution of species between levels is given in Table 2. With these parameters, level 4 species tend to have very low populations because there are barely sufficient resources coming up through the web to maintain

them. Species can also be classed as basal (having no prey), top (having no predators) or intermediate (having both predators and prey). A majority of species are intermediate for most reasonable parameter values. In fact the 10% of top species observed here is rather higher than the values in the examples in our previous papers. This is due to the rule used to define a link. Very weak interactions that would have been counted with our previous definition are discounted here using the criterion that the effort must be greater than 1%. We will consider in more detail elsewhere the way web statistics depend on the link definition. Also shown in Table 1 are the mean overlaps between species on each level (see equation (3)). This shows that considerable phenotypic diversity has accumulated in the species: only 2.6 out of 10 features are shared between species on level 1, and less than this on the higher levels.

The general patterns observed in real food webs are reproduced fairly well by the model. The values of quantities in real webs fluctuate greatly from web to web (see examples in Caldarelli *et al.* 1998). This can be put down to three factors. Firstly, the random nature of the evolutionary process leads to quite large fluctuations in web properties even if physical properties such as resource input and ecological efficiency are the same. In the model, this can be seen from the standard deviations in the web properties. Secondly, real webs are observed in different types of locations (lakes, deserts, estuaries etc.) that clearly do differ in terms of resource input and the nature of the limiting resource. Different groups of organisms exist in different locations that may differ in their ecological efficiency. In terms of the model, we began to consider the way the web properties changed with parameters such as R , λ and c in our previous papers. The third source of variation between the real webs is due to human observation. Different researchers use different definitions of what counts as a species, and what counts as a link. To what extent should similar species be lumped together? How often must a predation event be observed before a link is defined as being present? These questions are not straightforward, and they make detailed comparison between individual real webs, and between real and model webs difficult. Furthermore, while it is the case that the webs that we have generated are being compared to local communities, be they islands, lakes or forests, it is clear that the interaction between the community that we have evolved, and the species and individuals outside it, needs to be included in order to make the comparison with data valid. We hope to include the effects of immigration, and other such factors, in future work.

Table 1: Statistics on Food Web Structure

Result	Mean	Error in mean	Std. dev.
No. of species	59.1	0.3	8.6
Links per species	1.694	0.005	0.128
Av. level	2.313	0.002	0.059
Av. max. level	3.85	0.01	0.36
Basal species(%)	12.44	0.06	1.80
Intermediate species(%)	77.48	0.18	4.92
Top species(%)	10.06	0.16	4.45
Mean overlap level 1	0.260	0.002	0.047
Mean overlap level 2	0.105	0.001	0.019
Mean Overlap level 3	0.089	0.001	0.026

Table 2: Distribution of Species between Trophic Levels

Level	Number of Species	Std. dev.	Proportion of Species	Std. dev.
1	7.30	1.14	0.125	0.018
2	27.43	5.21	0.462	0.042
3	22.97	4.29	0.389	0.046
4	1.64	0.70	0.029	0.014

We have used the set of 800 stored webs to study in detail what happens when a single speciation event occurs. We performed 2000 independent speciation events on each of the starting webs and recorded the properties of each of the webs that arose when a new equilibrium situation was reached. Table 3 shows the statistics of these events. Events were defined as either addition (the child species survives and nothing goes extinct), substitution (the child species replaces the parent species but no other extinctions occur), no change (the child species goes extinct immediately, leaving the web the same as before the speciation event), and deletion (anything that is not addition, substitution or no change). In a deletion event, the new species must cause at least one species to become extinct that is not its parent. It can be seen approximately 89% of attempted speciations lead to no change, and the other 11% lead to a change in the web of some description.

We also show in Table 3 the origination rate (i.e. the probability that the newly created species survives), and the extinction rate (the average number of species excluding the new species that go extinct per speciation event). These quantities are both approximately 8.9%, and do not differ significantly from each other. In other words, originations balance extinctions on the timescale of a single speciation event. However Figure 2 shows that, on a long timescale, there is a slight increase in the total number of species present over the period 10000 to 100000 speciation events during which the stored webs were collected. Thus there is a very slight excess of originations to extinctions. Figure 8 shows the way the extinction and origination rate vary with time. In the initial part of the simulation up to time 10000, both rates are high and are decreasing significantly with time. For the period 10000 - 100000 used for the statistics, the two rates are relatively constant. They seem to leveling off at roughly 8%, which represents a moderate non-zero rate of turnover of species.

The standard deviations shown in Table 3 measure variations between the 800 stored webs. The quantities were averaged over the 2000 speciation events sampled for each stored web, and the mean and standard deviations were then taken over the 800 webs. For most quantities the standard deviation is small compared to the mean, but this is not true for the deletion probability and the extinction rate. When the distribution of extinction rates is considered across webs, there is a significant tail of high extinction rate webs that causes the large standard deviation. In contrast, the origination rate varies much less between webs. We intend to consider in more detail in future what properties of the stored webs make them more or less prone to

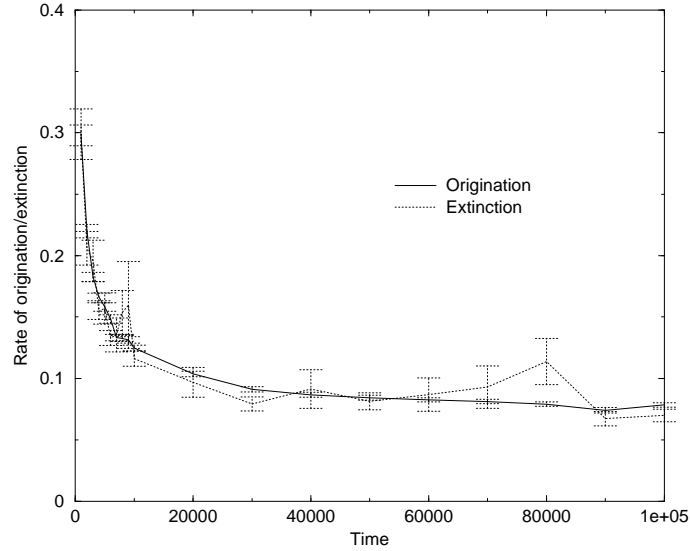


Figure 8: Rate of origination/extinction vs. time

extinctions.

Table 4 considers the way the trophic level of the parent species undergoing speciation affects the process of addition of new species. We have defined the level-specific origination rate as the probability that the child species survives given that the parent was on a particular level. This varies substantially between levels. It can be seen that the figure for level 2 is roughly equal to the average rate for the whole web given in Table 3, whereas the origination rate is significantly higher than average for level 3 and significantly lower for levels 1 and 4. Table 4 also gives the probability that the child ends up in each level given that it survives and given the level of the parent. Most of the child species occupy the same level as the parent (e.g. 92% of the children of level 1 species are also in level 1). There is a relatively small amount of movement between levels. The largest of the off-diagonal terms is the 29% probability of the child being in level 3 if the parent is in level 4. Given that most species enter the web on the same level as their parent, we can interpret the level-specific origination rates as measuring how easy it is to add species in a given level. The rate in level 1 is low because competition for external resources is strong, and because there is only one type of resource to compete for. For species on levels 2 and 3 there are many prey species on

Table 3: Probabilities of event types arising from a single speciation

Event type	Mean	Error in mean	Std. dev.
Addition	0.0417	0.0005	0.0152
Substitution	0.0230	0.0003	0.0093
Deletion	0.0425	0.0035	0.1000
No change	0.8928	0.0033	0.0932
Origination rate	0.08853	0.0008	0.0231
Extinction rate	0.08949	0.0038	0.1075

the level below from which to choose, and it becomes easier to find a niche in which to survive. The origination rate in level 4 is low, and we believe this is because level 4 species have a difficult time surviving due to lack of resources. Even a small amount of competition on this level is sufficient to drive the population below the minimum extinction threshold of 1. We have also measured the proportions of the species on each level as a function of time. These are roughly constant over the period 10000 - 100000, indicating that additions and deletions are roughly equal on each individual level.

Table 5 considers cases where a newly-created species survives, and asks what is the relationship between this species and any other species that go extinct as a consequence. The mean number of species affected is the mean number of species going extinct in each category as the result of the origination of one species. The mean probability of extinction is the probability that a species in a given category becomes extinct. The row ‘all species’ refers to all species previously in the web before the speciation event. ‘Parent’ refers to the parent of the new species. The ‘Predators’ and ‘Prey’ rows consider only species that are predators or prey of the new species. Note that the efforts of each species change during the population dynamics (see discussion in Drossel *et al.* 2001), so that predation links in the food web switch on and off as the population sizes change. For the purposes of this table, a species counts as a predator or prey if a link between the species is present at any time during the population dynamics (i.e. if the appropriate effort become

Table 4: The relationship of the trophic level of the child species to that of the parent, and the dependency of the origination rate on the parental level.

Child level:	1	2	3	4	Origination rate	Error	Std. dev.
Parent level							
1	0.92	0.00	0.02	0.06	0.0200	0.0005	0.0139
2	0.00	0.90	0.09	0.02	0.0893	0.0009	0.0256
3	0.00	0.01	0.97	0.02	0.1117	0.0012	0.0334
4	0.00	0.03	0.29	0.68	0.0638	0.0025	0.0642

greater than 1% for at least some of the time). Competitors are species that share at least one prey species with the newly-added species for at least some of the time during the population dynamics. Non-parental competitors are competitors other than the parent of the new species. Competitors' predators are species that are predators of the competitors of the new species.

From the top row, we see that an average of 0.773 species of all types become extinct per origination. This corresponds to a probability of only 1.4% that any random species goes extinct. In comparison, there is a 39.2% probability that the parental species goes extinct. This is due to the strong competition between parent and child. Since they differ by only one feature out of 10, the overlap value will be 0.9, and hence the α value will be very high. Typical overlaps between species on a level are between 0.089 and 0.26 (from Table 1), hence competition between parent and child species is much stronger than for most species pairs. Also, since they share nearly all features, the two species will often be adapted to feed on the same prey, which again increases competition above that typical for two species on the same level. For non-parental competitors, the extinction probability is 3.4%, which is about two and a half times higher than the average. Note that the statistical errors in all the quantities in Table 5 are small and are therefore not given. Thus, competition with the new species is a significant factor in causing extinction of existing species.

The extinction probability for prey of the new species is also significantly higher than average, indicating that new, well-adapted predators can drive their prey extinct. However this value is less than the value for non-parental

Table 5: The relationship of species going extinct to the newly added species.

Trophic relationship	Mean Number of Species Affected	Mean Probability of Extinction
All species	0.773	0.014
Parent	0.392	0.392
Predators	0.017	0.008
Prey	0.073	0.021
Competitors	0.499	0.147
Non-parental Competitors	0.108	0.034
Competitors' predators	0.082	0.014

competitors. In contrast, the extinction probability for predators of the new species is significantly less than average. This is to be expected, because a predator of a successful new species is also likely to be successful. The final case of competitors' predators was considered because one might expect that if competitors of the new species are driven extinct then predators of those species would also be more likely to go extinct than average. The result shows that the competitors' predators extinction rate is equal to the average rate, hence the effect we looked for is not apparent. One reason for this is that there are a rather large number of competitors' predators, hence the figure is bound to be rather close to the average. Also, species on the upper levels tend to have several prey, so that extinction of any one of these is not particularly important.

5 Discussion

The most distinctive feature of Webworld, and the aspect which sets it apart from other models in this field, is the attempt to model phenomena which occur on very different time scales. On the shortest time scale in the model, the number and types of species are fixed, as are the number of individuals that belong to these species. Only the amount of effort individuals of species

i put into preying on individuals of species j , f_{ij} , is allowed to vary. The choice of f_{ij} is a choice of foraging strategy, in our case given by the self-consistent solution of equations (2) and (4) (with the N_i fixed). On longer time scales the number and type of species is still fixed, but the number of individuals of a given species is now allowed to vary. This is the realm of traditional population biology, and in Webworld corresponds to determining the solutions of equation (1) in the long time limit. For simplicity, we have taken the death rate to be the same for all species. The choice of making the death rate equal to unity in equation (1) sets the timescale for the population dynamics. In all the simulations which we have carried out, we find that these solutions are steady states; no limit cycles or chaotic behaviour have been observed.

This point is worthy of further comment. A large fraction of the research which has been carried out in theoretical population dynamics has been concerned with models involving two or three species. There has been comparatively little work carried out on generic multispecies communities where a typical species will have several predators and several prey (whose number and identity may change with time) which is the situation of interest to us here. As a consequence, attention has focussed on the relatively simple equations found when only a few species are present, and especially on the phenomena of limit cycles and chaos frequently found in such equations. It is an open question as to whether these effects will be seen in food webs with a large number of species. One can argue that if one species is coupled to a large number of other species, these will act as a reservoir and blur out the details of the interactions that cause chaos, and so lead to a simpler dynamics. Alternatively, the adaptive nature of some aspects of the dynamics may lead to configurations where such behavior is less likely. This argument is similar to that put forward by Berryman & Millstein (1989a,b), who suggested that natural selection might favour parameter values which minimize the likelihood of chaotic dynamics. Of course, there may be other reasons why we have only seen steady states. Since the study of the long-time dynamics of equation (1) was not the ultimate goal of this investigation, we did not carry out a comprehensive investigation in the entire space of possible solutions, and it may be that some more complex behaviour does in fact exist. It might also be that the form of our equations has a particular structure which precludes more complicated long-time behaviour. Further work is required to decide which, if any, of these explanations is the correct one.

On the third, and longest, time scale the number and type of species is allowed to vary through a speciation mechanism. Effects of this kind have been modelled far less than have population dynamics or foraging mechanisms. One reason is that at the macroevolutionary level, such speciations will necessarily appear stochastic and modelling these will necessitate relatively long computer simulations. Another reason is that, at this stage in the development of the subject, there are few guidelines on how to model speciation. It is clear that we need to go beyond population dynamics, and give some internal characteristics to each species which are then allowed to vary with time according to an adaptive dynamics. We have chosen discrete features as these internal characteristics, but a set of continuous features might have also been a viable choice. It would be interesting to explore other ways of defining what is meant by a species in evolutionary models of this type. We always assume that the time for an ecosystem to reach a steady state is less than the time between speciation events. Thus it does not matter if the speciation rate varies with the number of species, or has other similar factors influencing it. In the Webworld model, ecological timescales are those which are longer than that defined by (1), but shorter than the time between speciation events. On the other hand, evolutionary timescales are those which are longer (typically, much longer) than the time between speciation events.

There has been a discussion in the literature between those opposed to and those favouring a functional response, g_{ij} , which is ratio-dependent (Berryman, 1992; Huisman & De Boer, 1997). Our main reason for choosing a ratio-dependent form was firstly, that it has many positive attributes from an ecological point of view (Berryman, 1992) and secondly, that it has fewer parameters associated with it. Indeed, our generalization of the ratio-dependent functional response to a multispecies food web (2), involves only two parameters: b and c . Nevertheless, it is not clear whether the precise form of the functional response matters much in the context of Webworld, where the ultimate state of interest is the one obtained after tens of thousands of speciation events. It may be that only general aspects such as the existence of strong competition, particularly between similar species, and the inclusion of a downward effect, as discussed earlier, are important. There may be a large degree of flexibility here, in the sense that the structure of the food web produced is insensitive to the precise form of g_{ij} , as long as the right qualitative structure is present. Further work is needed to clarify these points and to identify what the important ingredients are.

The food webs generated by Webworld, some of which are shown in Figs.

3-6, seem to evolve in a “natural” way when they are examined time-step by time-step. That is, the rules built into the model lead to consequences which can be interpreted according to rational criteria. Similarly, the consequences of a simple speciation event, which we have investigated in detail in this paper, seem very reasonable. Origination and extinction rates roughly balance on short time scales with slightly larger origination rates having an effect on longer time scales, child species tend to appear on the same level as parent species and there is strong competition between parent and child. All this is in line with expectations.

In summary, Webworld is a model which covers time scales varying from the very short, typified by changing foraging strategies, to the very long, required for evolutionary dynamics to reach a state where the number of originations and the number of extinctions balance on average. It gives results which are intuitively appealing and in broad agreement with food web data from real ecosystems. Many aspects of the model remain to be investigated, but we believe that it provides a realistic picture of the evolution of ecological communities which throws light on the nature of the basic mechanisms present in all such communities.

Acknowledgment

CQ wishes to thank EPSRC for the award of a postgraduate grant.

References

- Arditi, R. & Ginzburg, L.R. (1989). Coupling in predator-prey dynamics: ratio-dependence. *J. Theor. Biol.* **139**, 311-326.
- Arditi, R. & Michalski, J. (1995). Nonlinear food web models and their responses to increased basal productivity. In: *Food webs: integration of patterns and dynamics* (Polis, G.A. & Winemiller, K.O., eds), pp. 122-133, Chapman & Hall, London.
- Bak, P. & Sneppen, K. (1993). Punctuated equilibrium and criticality in a simple model of evolution. *Phys. Rev. Lett.* **71**, 4083-4086.
- Bastolla, U., Lässig, M., Manrubia, S.C. & Valleriani, A. (2000). Diversity patterns from ecological models at dynamical equilibrium. eprint: arXiv: nlin.AO/0009025.
- Beddington, J. (1975). Mutual interference between parasites or predators and its effect on searching efficiency. *Anim. Ecol.* **51**, 597-624.
- Berryman, A.A. & Millstein, J.A. (1989a). Are ecological systems chaotic — and if not, why not? *Trends Ecol. Evol.* **4**, 26-28.
- Berryman, A.A. & Millstein, J.A. (1989b). Avoiding chaos — reply. *Trends Ecol. Evol.* **4**, 240-240.
- Berryman, A.A. (1992). The origins and evolution of predator-prey theory. *Ecology* **73**, 1530-1535.
- Caldarelli, G., Higgs, P.G. & McKane, A.J. (1998). Modelling coevolution in multispecies communities. *J. Theor. Biol.* **193**, 345-358.
- Cohen, J.E. (1990). A stochastic theory of community food webs VI - Heterogeneous alternatives to the cascade model. *Theor. Pop. Biol.* **37**, 55-90.
- Cohen, J.E., Briand, F. & Newman, C.M. (1990). *Biomathematics* Vol. 20. Community food webs, data and theory. Springer Verlag, Berlin.
- Drossel, B. (2001). Biological evolution and statistical physics. eprint: arXiv:cond-mat/0101409.
- Drossel, B., Higgs, P.G. & McKane, A.J. (2001). The influence of predator-prey population dynamics on the long-term evolution of food web structure. *J. Theor. Biol.* **208**, 91-107.
- Emlen, J.M. (1984). *Population biology*. Macmillan, New York.
- Goldwasser, L. & Roughgarden, J. (1993). Construction and analysis of a large Caribbean food web. *Ecology* **74**, 1216-1233.
- Hall, S.J. & Raffaelli, D. (1991). Food web patterns: lessons from a species-rich web. *J. Anim. Ecol.* **60**, 823-842.

- Hallam, T.G. (1986). Community dynamics in a homogeneous environment. In: *Mathematical ecology*. Biomathematics Vol. 17. (Hallam, T.G. and Levin, S.A., eds), pp. 241-285, Springer-Verlag, Berlin.
- Hastings, A. & Powell, T. (1991). Chaos in a three-species food chain, *Ecology* **72**, 896-903.
- Hofbauer, J. & Sigmund, K. (1998). *Evolutionary games and population dynamics*. Cambridge University Press, Cambridge.
- Holling, C.S. (1959). Some characteristics of simple types of predation and parasitism. *Can. Entomol.* **91**, 385-398.
- Huisman, G. & De Boer, R.J. (1997). A formal derivation of the Beddington functional response, *J. Theor. Biol.* **185**, 389-400, and references therein.
- Lässig, M., Bastolla, U., Manrubia, S.C. & Valleriani, A. (2001). The shape of ecological networks. eprint: arXiv:nlin.AO/0101026.
- Logofet, D.O. (1993). *Matrices and graphs: stability problems in mathematical ecology*. CRC Press, London.
- Martinez, N.D. & Lawton, J.H. (1995). Scale and food web structure — from local to global. *Oikos* **73**, 148-154.
- May, R.M. (1974). *Stability and complexity in model ecosystems*. Monographs in population biology, Vol. 6. Princeton University Press, Princeton. Second edition.
- McCann, K. & Yodzis, P. (1994). Biological conditions for chaos in three-species food chain. *Ecology* **75**, 561-564.
- Parker, G.A. & Maynard Smith, J. (1990). Optimality theory in evolutionary biology. *Nature*. **348**, 27-33.
- Pielou, E.C. (1977). *Mathematical ecology*. Wiley, New York, Second edition.
- Pimm, S.L. (1982). *Food webs*. Chapman & Hall, London.
- Post, D.M., Conners, M.E. & Goldberg, D.S. (2000). Prey preference by a top predator and the stability of linked food chains. *Ecology* **81**, 8-14, and references therein.
- Reeve, H.K. & Dugatkin, L.A. (1998). Why we need evolutionary game theory. In: *Game theory and animal behaviour* (Dugatkin, L.A. & Reeve, H.K., eds), pp. 304-311. Oxford University Press, Oxford.
- Roughgarden, J. (1979). *Theory of population genetics and evolutionary ecology*. Macmillan, New York.
- Solé, R.V., Manrubia, S.C., Benton, M. & Bak, P. (1997). Self-similarity of extinction statistics in the fossil record. *Nature* **388**, 764-767.
- Stephens, D. W. & Krebs, J. R. (1986). *Foraging theory*. Princeton University Press, NJ.

Svirezhev, Yu.M. & Logofet, D.O. (1983). *Stability of biological communities*.
Mir Publishers, Moscow.